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Estimating seed production of three *Setaria* species in row crops

Frank Forcella
Corresponding author. North Central Soil Conservation Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, 803 Iowa Avenue, Morris, MN 56267; forcella@morris.ars.usda.gov

Nathalie Colbach
Station d'Agronomie, INRA, BV 1540, 17 rue Sully, 21034 Dijon Cedex, France

George O. Kegode
Department of Agronomy and Plant Genetics and West Central Research and Outreach Center, University of Minnesota, Morris, MN 56267. Present address: Department of Plant Sciences, North Dakota State University, Fargo, ND 58101

Seed production of weedy species of *Setaria* in crops of *Zea mays* and *Glycine max* was studied for 2 yr in western Minnesota and eastern South Dakota. Viable seed production was curvilinearly related to panicle length. A 100-mm-long panicle of *S. pumila, S. faberi,* and *S. viridis* produced 129, 323, and 851 viable seeds, respectively. Values were consistent across years, crops, and herbicide treatments. Frequency distributions of panicle lengths of all panicles within a population closely followed nonlinear Weibull functions and were stable across years and crops but not species or herbicide treatment. Positive skewness of these distributions decreased, and median panicle size (mm) increased, in the following order: *S. viridis* (41), *S. pumila* (52), and *S. faberi* (78). Postemergence herbicides applied at full label rates increased skewness and reduced median panicle size (to 11 mm) and seed production of *S. viridis.* Skewness lessens the reliability of using average panicle size as a measure of seed production for the entire population. However, integration of panicle size–frequency and panicle size–fecundity relationships provided estimates of the number of seeds per panicle that were more representative of the population than the statistical average panicle. These estimates were 52, 242, and 246 seeds per panicle for *S. pumila, S. viridis,* and *S. faberi,* respectively. Multiplication of these values by panicle densities generated seed production estimates that were similar to actual counts of seeds. *Setaria* seed production tended to be higher in *Z. mays* than in *G. max* only because of higher plant and panicle densities. Early-maturing panicles tended to be larger than those maturing later, but seed viability generally was stable across maturity times.

Nomenclature: Soybean, *Glycine max* (L.) Merr.; giant foxtail, *Setaria faberi* (L.) Beauv. SETFA; yellow foxtail, *S. pumila* (Poir.) Roem. & Schult. (= *S. glauca* (L.) Beauv.), SETLU; green foxtail, *S. viridis* (L.) Beauv. SETVI; corn, *Zea mays* L.

Key words: Seed dispersal, seed rain.

Setaria species are major grass weeds of arable crops in North America. Although these species are known to produce many seeds (Santlemann et al. 1963; Schreiber 1965; Vanden Born 1971), the magnitude of production in crops and factors regulating production are poorly understood. The ability to predict seed production of *Setaria* that escape control would help to improve management decisions because long-term management of *Setaria* requires maintenance of seedbank densities as low as possible. We currently do not have the ability to easily estimate seed production by uncontrolled *Setaria.*

Inability to estimate *Setaria* seed production can be attributed, in part, to relatively few field studies of this topic. At 130 plants m^{-2}, well-watered monocultures of *S. viridis* in Manitoba produced 2,720 to 3,050 seeds per plant (353,000 to 396,500 seeds m^{-2}), and *S. pumila* monocultures produced 520 to 890 seeds per plant (67,600 to 115,700 seeds m^{-2}) (Nadeau and Morrison 1986). In *Z. mays* not treated with herbicides, a population of *S. viridis*[1] of 358 plants m^{-2} in Minnesota produced 25,600 apparently viable seeds m^{-2} in one year, and during the following year a population of 552 plants m^{-2} produced 14,000 seeds m^{-2} (Forcella et al. 1996b). In untreated *G. max*, 18 *S. faberi* plants m^{-2} in Missouri produced 6,070 seeds m^{-2} in one year, and 44 plants m^{-2} produced 11,400 seeds m^{-2} the next year (Defelice et al. 1989). In Michigan, 13 to 129 *S. faberi* plants m^{-2} produced 33,000 to 98,000 seeds m^{-2} in a manner quadratically related to plant density (Fausey et al. 1997).

S. faberi plants that survived reduced rates of postemergence herbicide applications in *G. max* produced about 800 seeds per plant (Defelice et al. 1989). Herbicides nearly eliminated panicle production in this study, but in panicles that did develop, the number of seeds per panicle was not reduced. In another *G. max* study, a single untreated *S. faberi* m^{-2} in Arkansas produced 3,167 seeds (Biniak and Aldrich 1986). Application of herbicides at first anthesis reduced panicle densities considerably but only modestly reduced seeds per panicle. Later herbicide applications (10 to 24 d after first heading) sometimes decreased panicles m^{-2} but never reduced seeds per panicle.

In *Beta vulgaris* L. (sugarbeet), *Echinochloa crus-galli* (L.) Beauv. (barnyardgrass) densities ranging from 0.1 to 100 plants m^{-1} of crop row reduced the number of *E. crus-galli* panicles per plant from more than 80 to less than 20 (Norris 1992b). However, these same *E. crus-galli* densities did not influence the average number of seeds per panicle. Thus, competition appears to influence grass seed production in

[1] In west-central Minnesota, *S. viridis* populations consistently exist as mixtures of two taxa recognized by WSSA: *S. viridis robusta-purpurea* Schreiber and *S. viridis robusta-alba* Schreiber. We suspect that these forms probably are merely color variants of the same taxon. Thus, we refer to both simply as *S. viridis.*

the same manner as low rates of postemergence herbicides (Norris 1992b; Biniak and Aldrich 1986), that is, reduced panicle density but unaltered panicle fecundity.

Because seeds of *Setaria* are produced in elongated and densely packed panicles, these infructesences provide a relatively convenient means by which to study seed production. There are at least four methods with which *Setaria* panicles can be used to estimate seed production. These methods, ranked from most to least laborious, are panicle harvest, panicle fecundity, panicle averaging, and panicle frequency. The panicle harvest method involves harvesting all panicles from a specific area prior to seed dispersal, stripping all seeds from the panicles, and calculating seed production on a standard unit-area basis.

The panicle fecundity method is an abbreviation of the first procedure: (1) a mathematical relationship is developed between panicle length and number of seeds (e.g., seed number per mm of panicle), (2) all panicles within a plot are measured, (3) lengths of each panicle are multiplied by seed number per mm of panicle, and (4) estimated seed numbers for each panicle are summed for the entire plot.

The panicle averaging method involves counting the number of panicles within a unit-area and multiplying the sum by the number of seeds on an average panicle. This procedure assumes that panicle sizes are normally distributed and that there is a linear relationship between panicle size and seed number.

The panicle frequency technique is a condensed version of the second method and assumes that panicle sizes are not necessarily normally distributed and number of seeds per panicle is not necessarily linearly related to panicle length. In this method, all panicles within a plot are counted, but not measured, and then multiplied by two variables. The first variable is a factor that describes panicle size for the population, and the second variable is seed number per mm of panicle. Panicle size for the population can be summarized by a frequency distribution. Norris (1992a) suggested that the frequency distribution for *E. crus-galli* may be stable across environments. If true, seed production of a stand could be estimated simply by counting total panicles present and employing the appropriate formulae for frequency distribution and seed number per mm of panicle.

The assumptions of a linear vs. nonlinear seed number–panicle length relationship (Figure 1A) and a normal vs. skewed frequency distribution for panicle lengths (Figure 1B) can have important consequences for estimating seed production. For example, using the four possible combinations of relationships shown in Figure 1 for seed number–panicle length and panicle size frequency distributions (i.e., linear + normal, linear + skewed, nonlinear + normal, and nonlinear + skewed), calculated seed production for a population of 100 panicles would be 8,480, 10,356, 5,065, and 8,041 seeds m^{-2}, respectively. Although this example was chosen to emphasize extreme differences, it illustrates the potential problems associated with making specific assumptions for estimations of weed seed production.

An alternative and indirect method of estimating seed production involves the use of seed traps (Forcella et al. 1996a, 1996b). Traps capture fallen seeds within a specific unit-area, and the seed numbers for each unit-area can be extrapolated to standard units, such as a square meter or hectare. However, use of seed traps can entail high labor requirements.

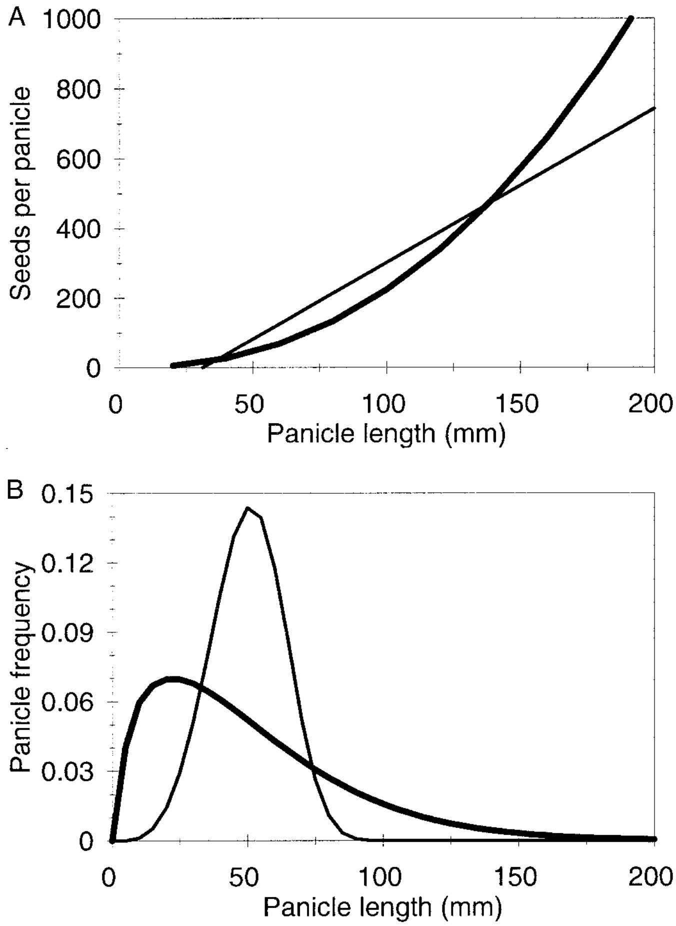

FIGURE 1. (A) Idealized linear (thin line) and nonlinear (heavy line) relationships between the number of seeds borne on *Setaria* panicles and the lengths of those panicles; mean seed number is the same for both curves. (B) Idealized normal (thin line) and skewed (heavy line) distributions of *Setaria* panicle lengths within a population; mean panicle lengths are identical for both curves.

Our objectives were to explore and compare the four panicle-based methods of estimating production of apparently viable seed of *S. faberi, S. viridis,* and *S. pumila* in *Z. mays* and *G. max.* We also examined seasonal variability in the production of viable and nonviable seeds, and for *S. viridis* we determined the influence of herbicide application on these relationships.

Materials and Methods

Field Sites and Plots

Experiments were conducted in 1993 and 1994 at three sites, each dominated by a different *Setaria* species. The *S. viridis* site was at the University of Minnesota, West Central Experiment Station, Morris, MN, and was situated on an Aastad clay loam soil (Pachic Udic Haploboroll, fine, mixed, mesic). The *S. faberi* site was located at the University of Minnesota, Southwest Experiment Station, Lamberton, MN, on a Normania clay loam (Aquic Haplustoll, fine loamy, mixed, mesic). Finally, the *S. pumila* site was at the U.S. Department of Agriculture, Agricultural Research Service, Eastern South Dakota Soil and Water Research Farm, Brookings, SD, on a Vienna loam (Udic Haploboroll, fine loamy, mixed).

At each site, *Z. mays* and *G. max* plots were located in previously established long-term experimental rotations of these two crops. Seedbeds were prepared with a field cultivator and crops sown on May 18, 1993, and May 23, 1994, in Morris; May 14 and 26 (*Z. mays* then *G. max*), 1993, and May 13 and 27, 1994, in Lamberton; and May 17, 1993, and May 10, 1994, in Brookings in soil that had been moldboard plowed during the previous autumn. Crops were sown at standard densities, about 75,000 seeds h^{-1} for *Z. mays* and about 350,000 seeds ha^{-1} for *G. max*. Crop rows were 76 cm wide. *Z. mays* plots were fertilized with the equivalent of 110 kg N ha^{-1}. *G. max* plots were not fertilized.

Plot size was 9.1 by 19.8 m in Morris and 6.1 by 15.2 m in both Lamberton and Brookings. There were four plots per crop in Morris and 3 plots per crop elsewhere. Plots were arranged in blocks, with each block containing randomly positioned plots of *Z. mays* and *G. max*.

All experimental *Setaria* plants arose from "natural" seed populations. Once *Setaria* seedlings had emerged, all weeds, except the desired species, were removed by hand weeding in a single centrally located *Setaria* subplot in each plot. The subplots were 2 rows (1.52 m) wide and 3 m long. In each subplot, *Setaria* plants were confined to a 10-cm band centered on and parallel to the crop row. The row middles were cultivated and subplots further cleaned by hand weeding as needed. Existing densities of early-emerging *Setaria* seedlings were used. Late-emerging seedlings were removed weekly, so that all experimental plants were present in the crop for the entire season.

An additional set of plots was established at Morris in each year. These plots were adjacent to the original plots and identical in size, number, and management, except that they were sprayed postemergence with label rates of nicosulfuron plus 4% v/v of 28% liquid nitrogen and 1% v/v crop oil concentrate in *Z. mays* and sethoxydim plus 1% v/v crop oil concentrate in *G. max*. Herbicides were applied with a tractor-mounted 3.1-m boom with flat fan nozzles that delivered 187 L ha^{-1} at 270 kPa.

Panicle Collection and Processing

When panicles began to mature, and at weekly intervals thereafter, all mature panicles were collected from each subplot. We believe that this protocol allowed few seeds to shed prior to panicle collection.[2] Five randomly selected panicles, when available, from each sample were bagged separately and later measured for panicle length and seed number. Seed number was determined after "debearding" panicles by quickly burning bristles with an alcohol flame, stripping seeds from the panicle, and separating apparently viable (heavy, sound, or full) and nonviable (empty or broken) seed with an airflow seed cleaner. Apparently viable seeds were counted with an automated seed counter, whereas nonviable seeds were counted by hand. The remaining panicles in each sample were debearded, stripped, and cleaned, and apparently viable seeds were counted. Total seed production was calculated by summing seed numbers of all panicles and dividing by subplot area.

Numbers of *Setaria* reaching anthesis were counted in each 3-m crop row of each subplot each year. Values were transformed to average density per square meter.

Statistical Analyses

Linear and nonlinear equations were examined to relate panicle length and seed number (Anonymous 1994). Several equations related panicle length and seed number, and many resulted in high values for attributable variability (r^2). The choice of one equation over another was somewhat arbitrary. Our criteria were that a chosen equation captured the main trend of the data, was close to zero at the origin (0 seeds at 0 mm panicle length), contained no more than two calculated coefficients, and possessed a relatively high r^2 value. Regression coefficients were compared between treatments (crops, years, herbicide application) within species by testing for "homogeneity of slopes" (Gomez and Gomez 1984). Data were combined across treatments when coefficients did not differ significantly ($P > 0.05$).

If panicle lengths were normally distributed, the mean could be calculated and used to estimate seed numbers produced in average panicles. Preliminary analyses showed that panicle size distributions were asymmetric. For this reason, frequencies of panicles of known lengths were calculated for each species, year, and crop. For example, Figure 2 shows the cumulative frequencies of *S. faberi* panicles sizes from *Z. mays* and *G. max* plots in both 1993 and 1994.

Weibull Frequencies

For each species, crop, year, and herbicide application (*S. viridis* only), cumulative panicle frequencies were fit to a nonlinear model (Weibull function) of the following form:

$$y = 1 - exp(-a\, x^b) \qquad [1]$$

where y is cumulative frequency, x is panicle size (mm), and a and b are coefficients depending on species, crop, year, and herbicide application. Thus, cumulative frequency, y, is nil when panicle size is zero and approaches unity when panicles are infinitely long.

Coefficient a in Equation 1 was replaced by a function that was dependent on coefficient b and a new variable, x_{50}, which is the median panicle size (50% of panicles smaller and larger than x_{50}). This function has the following form:

$$a = ln\ 2/x_{50}{}^b \qquad [2]$$

After estimating b and x_{50} with the NLIN procedure of SAS (1989), x_{10} and x_{90} (panicle sizes > 10 and 90% of the total sample) also were calculated by the following formulae:

$$x_{10} = (-ln\ 0.9/a)x^{1/b} \qquad [3]$$

[2] This method may be flawed because if panicles are harvested early, some seeds may be immature and nonviable, whereas if older panicles are harvested, some seeds may have shed before sampling. These possibilities were prevented during an additional year of study, 1996, in the same Morris plots used in 1993 and 1994. Both *S. viridis* and *S. pumila* panicles were covered by white translucent mesh bags after anthesis but before seed shed. Panicles were harvested at maturity, their lengths measured, and viable seeds counted.

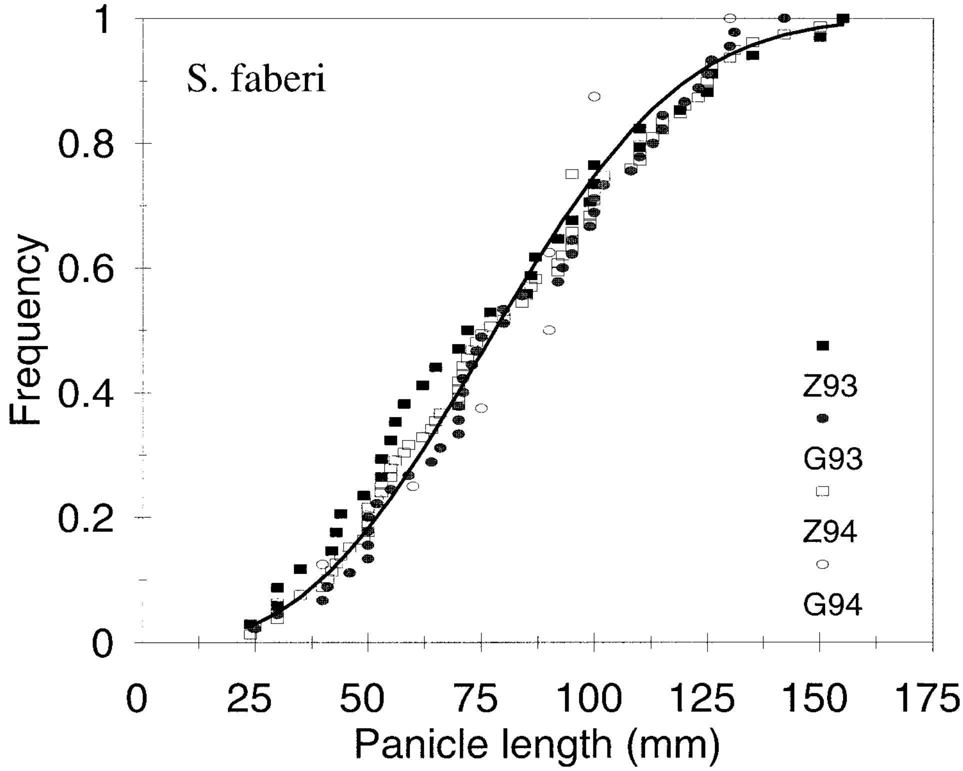

FIGURE 2. Cumulative frequency distributions of *S. faberi* panicle lengths in *Z. mays* and *G. max* crops during 1993 and 1994 in comparison to a best-fit Weibull function (solid line) describing the general relationship.

$$x_{90} = (-ln\ 0.1/a)x^{1/b} \qquad [4]$$

The value $x_{90} - x_{10}$ is an expression of the dispersion of panicle sizes; that is, the larger this value, the higher the dispersion.

For each parameter (b, x_{50}, and $x_{90} - x_{10}$), the estimated values were used as output variables in a linear model, with species, crop, year, and herbicide application as input variables. Thus, the parameter estimate = intercept + species effect + crop effect + year effect + herbicide effect + species × crop interaction + species × year interaction + crop × year interaction + year × herbicide interaction + error.

The final model contained only those input factors (above) for which the estimated effects were significantly different from zero at P = 0.05. If P > 0.05, the effect of the factor was considered insignificant. The model was analyzed with the GLM procedure of SAS. The statistical condition of homogeneity of variance (Box et al. 1978) was consistently fulfilled, and thus no parameter transformations were necessary. Finally, parameter variances were those estimated by the NLIN procedure (SAS) simultaneously with parameter estimates for b and x_{50}. In the cases of x_{10} and x_{90}, the variances were calculated using the variance–covariance matrix of b and x_{50} and the derivatives, db/dx_{10}, db/dx_{90}, dx_{50}/dx_{10}, and dx_{50}/dx_{90}, in the following manner:

$$\begin{aligned}&\text{variance}(dx_{10})\\&= db/dx_{10} \times (db/dx_{10} \times \text{var}(b) + dx_{50}/dx_{10} \times \text{covar}(b, x_{50}))\\&\quad + dx_{50}/dx_{10} \times (db/dx_{10} \times \text{covar}(b, x_{50}) + dx_{50}/dx_{10} \times \text{covar}(x_{50})). \qquad [5]\end{aligned}$$

If Weibull functions existed that related panicle sizes and frequencies, they could be used to categorize simple counts of panicle densities into panicle numbers within each size class. Average number of seeds produced per size class could be calculated and multiplied by the number of panicles in that size class. Summation of these products would provide a quick and simple estimate of total seed production within a specific area. This manner of calculating seed production will be referred to hereafter as the "panicle frequency" method.

Total Seed Production

For each year total seed production in each plot was estimated by the panicle fecundity, panicle averaging, and panicle frequency methods. For panicle fecundity, we multiplied the species-specific equation describing seed number per unit of panicle length by the length of each panicle in each plot and summed the products. For panicle averaging, we calculated average seed number per panicle and multiplied by the number of panicles in each plot. For Weibull panicle frequencies, we integrated three components of seed production: (1) number of panicles per plot, (2) the species-specific equation describing panicle size frequency distributions, and (3) the species-specific equation describing seed number per unit of panicle length. These estimates were compared to values of seed production calculated from total panicle harvests in each plot. Comparisons were made by calculating percentage deviation of estimates from total panicle harvest. Deviations could be positive (overestimation) or negative (underestimation). The method with the lowest overall absolute percent deviation was assumed to be the most accurate method.

Results and Discussion

Panicle Numbers and Seed Viability

During 1993 and 1994, the number of panicles harvested, measured for length, and stripped of apparently viable seeds was 536, 1,186, and 2,162 for *S. faberi*, *S. viridis*, and *S. pumila*, respectively. The numbers of panicles measured and assessed for viable and nonviable seeds were 87, 294, and 209 for the same species. During 1996 in Morris, 131 and 156 mesh-enclosed *S. viridis* and *S. pumila* panicles also were examined.

Overall, apparent seed viabilities in 1993 and 1994 were 63 and 75% for *S. faberi*, 64 and 75% for *S. viridis*, and 65 and 74% for *S. pumila*. Analysis of variance (ANOVA) indicated that differences between years were not significant ($P > 0.05$). Similarities among species in apparent viability were remarkable. Observed viability percentages for *S. viridis* were similar to those reported for a different site in Minnesota. At that site, viability of *S. viridis* seed recovered from seed traps was 79% in each of 2 yr, but seed viability varied greatly for broadleaf species between years (Forcella et al. 1996b).

Plant Densities

Averaged over *Setaria* species, *Z. mays* and *G. max* plots contained 40 and 35 panicles m^{-2} ($P > 0.05$) in 1993 and 4 and 1 panicles m^{-2} ($P < 0.05$) in 1994. The trend for slightly greater *Setaria* panicle density in *Z. mays* than in *G. max* was due to greater *Setaria* plant densities in *Z. mays* (data not shown). Thus, crop type appeared to have no consistent effect on the number of panicles produced. Herbicides also influenced only the density of *S. viridis* plants, not the relationship between *S. viridis* panicles and plant densities. Thus, panicle density could be related to plant density regardless of crop type and herbicide application.

Panicle density increased as a square-root function of *Setaria* density for each species, which suggested density-dependent production of panicles, as was observed for *S. faberi* in Michigan (Fausey et al. 1997) and for seed production and plant density of *S. viridis* in Minnesota (Forcella et al. 1996a). Equations and associated statistics that described panicles m^{-2} (P) as functions of plants m^{-2} (D) were as follows: *S. faberi*, $P = -19.4 + 22.8 \times D^{0.5}$ ($r^2 = 0.89$, $P = 0.01$), *S. viridis*, $P = -6.6 + 13.6 \times D^{0.5}$ ($r^2 = 0.41$, $P = 0.02$), and *S. pumila*, $P = -36.7 + 41.1 \times D^{0.5}$ ($r^2 = 0.74$, $P = 0.01$). These equations cannot be used when *Setaria* densities are < 1 plant m^{-2}. The relatively poor relationships between panicle and plant density for *S. viridis* and *S. pumila* ($r^2 < 0.75$) probably were due to environmental effects other than crop type and herbicide application, which indicated that *Setaria* plant density may not always be a reliable predictor of panicle production.

Panicle Fecundity

For each species, there was a consistent curvilinear relationship between panicle length and total number of apparently viable seeds (Figure 3; Table 1). Data were pooled across crops and years because there were no differences between coefficients (seeds per transformed unit-length of panicle) and y-intercepts for *Setaria* growing in *Z. mays* or *G. max*, growing in 1993 or 1994, or growing in plots treated or not treated with postemergence herbicides. Panicles of *S. viridis* produced many more seeds per unit length than those of either *S. faberi* or *S. pumila*. For example, a 100-mm-long panicle of *S. viridis* was estimated to produce 851 apparently viable seeds, whereas comparable panicles for *S. faberi* and *S. pumila* were estimated to produce 323 and 129

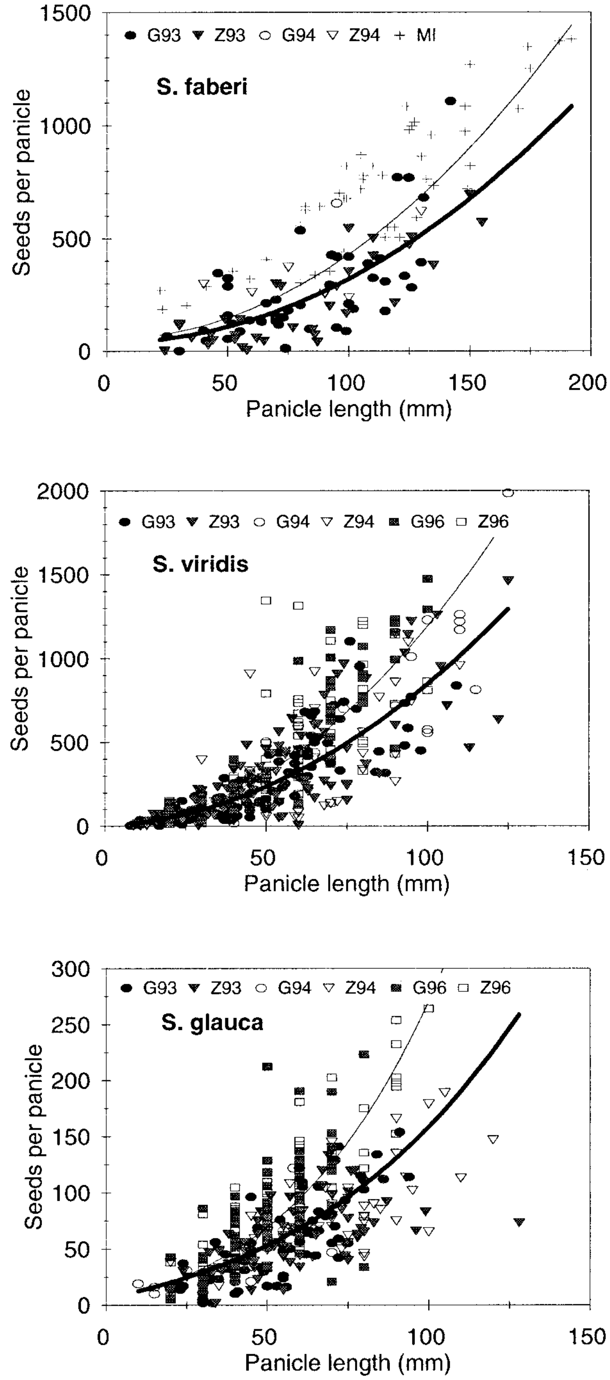

FIGURE 3. Relationships between numbers of apparently viable seeds produced on panicles and the length of the panicles for *S. faberi*, *S. viridis*, and *S. pumila* growing in *Z. mays* (Z93, Z94) and *G. max* (G93, G94) in 1993 and 1994. Fitted lines derived from equations listed in Table 1. Heavy lines are associated with the 1993 and 1994 data. Light lines are associated with regressions for *S. faberi* from Michigan (MI) (Fausey et al. 1997) and *S. viridis* and *S. pumila* using seeds and panicles enveloped in translucent mesh bags to prevent preharvest losses of mature disarticulating seed during 1996 (G96, Z96).

Table 1. List of regression coefficients for equations that described the number of apparently viable seeds as a function of panicle length (x, in mm) for *S. faberi*, *S. viridis*, and *S. pumila* (data combined for *Z. mays* and *G. max* and for 1993 and 1994). Values in parentheses represent coefficients for analogous relationships derived from data of Fausey et al. (1997) for *S. faberi* and from *S. viridis* and *S. pumila* panicles enclosed in mesh bags during 1996 (cf. Figure 3).

	S. faberi	*S. viridis*	*S. pumila*
Coefficient	Parameter values		
a	**38.510**	**1.7304**	**1.3449**
	(293.06)	(0.8613)	(0.9522)
b	**0.0284**	**0.2744**	**0.3722**
	(0.0317)	(0.3369)	(0.4649)
r^2	**0.55**	**0.67**	**0.52**
	(0.77)	(0.63)	(0.63)
Seed number =	$a + bx^2$	$(a + bx)^2$	$exp(a + bx^{0.5})$

Table 2. Statistical summary for analysis of variance of frequencies of panicle length of *S. faberi*, *S. viridis*, and *S. pumila* using a frequency distribution equation (Weibull function). (A) Attributable variability and probabilities that the effects of species (*S. faberi*, *S. viridis*, and *S. pumila*), crop (*Z. mays* or *G. max*), year (1993 or 1994), and herbicide (applied or absent) are greater than naught (null hypothesis = 0). (B) Parameter estimates of factors (species and herbicide) for the Weibull function (see text) that were significant for *S. faberi*, *S. viridis*, and *S. pumila*.

A Parameters	r^2	Null hypothesis	Factors: Species	Crop	Year	Herbicide
			P			
b	51	P (H = 0)	0.048	NS[a]	NS	NS
x_{50}	87	P (H = 0)	0.001	NS	NS	0.001
$x_{90} - x_{10}$	94	P (H = 0)	0.013	NS	NS	0.004

B Factors: Species	Herbicide	Parameters: *b*	x_{50}	$x_{90} - x_{10}$
S. faberi	No	2.77 a	78 a	84 a
S. pumila	No	2.69 a	52 b	57 ab
S. viridis	No	1.87 ab	41 c	66 b
S. viridis	Yes	1.49 b	11 d	20 c

[a] Abbreviation: NS, not significant.

viable seeds, respectively. Thus, the number of seeds produced by large panicles was more than twice as great for *S. viridis* than for *S. faberi* and over six times greater for *S. viridis* than for *S. pumila*.

For *S. faberi*, the relationship between seeds per panicle and panicle length in Minnesota showed the same curvilinear trend as that for *S. faberi* in Michigan (Figure 3). The small number (48) of panicles selected for the Michigan study (Fausey et al. 1997) often were longer than those from Minnesota. Similarly, the number of seeds per mm of panicle length also tended to be higher for *S. viridis* and *S. pumila* that were sampled in 1996 as opposed to those studied during 1993 and 1994 (Figure 3). The panicles studied in 1996 were enclosed in mesh bags during maturation, which prevented loss of seeds by shedding, and this may have accounted for the higher seed numbers. As in the preceding years, there were no differences in seeds per mm of panicle length between panicles collected from *Z. mays* and *G. max* plots during 1996. Curvilinear equations were developed for each set of independent panicle size–seed number data for each species (Figure 3). Although these differed from those derived from the 1993 and 1994 data, they showed the same trends.

The regression equations for each *Setaria* species had positive values for y-intercepts, implausibly implying that panicles measuring 0 to 1 mm long produced viable seeds, for example, 39, 3, and 3 seeds per panicle for *S. faberi*, *S. viridis*, and *S. pumila*, respectively. In our study, however, panicles shorter than 10 mm were observed only rarely. Consequently, positive values for y-intercepts probably have no adverse consequences for estimating *Setaria* seed production.

The relatively strong allometric relationships between panicle size and seed numbers, regardless of crop type, year (1993 and 1994), or herbicide application (for *S. viridis*), are important. The consistency of these relationships suggests that seed production of escaped *Setaria* can be estimated at any time between *Setaria* anthesis and crop harvest and under many different environmental conditions simply by counting panicles and measuring panicle lengths in representative areas of a field.

Panicle Averaging

The average numbers of apparently viable seeds per panicle for *S. viridis*, *S. faberi*, and *S. pumila* were 319, 256, and 64, respectively. For herbicide-treated *S. viridis*, the average number of viable seeds per panicle was 175. These averages, however, were for skewed distributions (discussed in the following section).

Weibull Panicle Frequencies

Frequencies of panicle sizes for all *Setaria* species fit a single equation (Figure 2) with high r^2 values, although the equation's coefficients differed for each species but not for populations growing in *Z. mays* and *G. max* or growing in different years (Table 2). For *S. viridis*, herbicides had a significant effect on panicle size frequencies, and these effects will be discussed in a following section.

The frequency distributions of panicle sizes for each *Setaria* species (Table 2; Figure 2) also corresponded to independently observed frequencies of *Setaria* panicle sizes. Regressions of frequencies of *S. faberi* panicle sizes (sampled by Fausey et al. 1997) and *S. viridis* and *S. pumila* panicle sizes (sampled in Minnesota during 1996) against predictions from the appropriate equations in Table 2 resulted in r^2 values of 0.81, 0.88, and 0.91 for *S. faberi*, *S. viridis*, and *S. pumila*, respectively. In each case, regression slopes were near unity (0.91, 1.09, and 1.10), y-intercepts were close to zero, and $P < 0.005$, all of which indicate wide applicability of the Weibull frequency distributions of *Setaria* panicle sizes listed in Table 2.

Species and Herbicide Effects

Median panicle size (x_{50}) was highest for *S. faberi* (78 mm), intermediate for *S. pumila* (52 mm), and lowest for *S. viridis* (41 mm). The dispersion of panicle sizes ($x_{90} -$

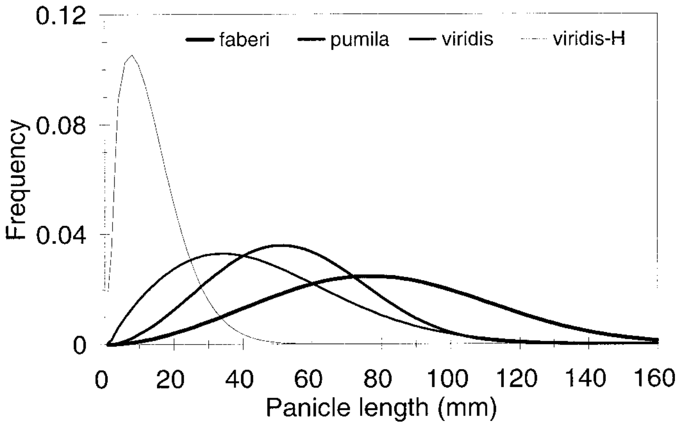

FIGURE 4. Comparison of frequency distributions of panicle lengths for *S. faberi*, *S. pumila*, and *S. viridis* and herbicide-treated *S. viridis* (*viridis*-H). Lines are derived from equations listed in Table 2.

x_{10}) tended to follow the same trend. Thus, panicle lengths were generally largest and most variable for *S. faberi* and smallest and least variable for *S. viridis.* The distribution of this latter population also was the least symmetric, as indicated by the lowest *b* value in Table 2. The effects of postemergence herbicides can be seen by comparing treated and nontreated *S. viridis.* Within this species, panicles were smaller, less variable, and more asymmetric when postemergence herbicides were applied (Figure 4). Within populations of each species, the percentages of small panicles ($\leq$ 50 mm) were 18, 46, 63, and 99% for *S. faberi, S. pumila, S. viridis,* and *S. viridis* (with herbicide), respectively. Percentages of medium-sized panicles (51 to 100 mm) were 57, 52, 34, and 1%, whereas values for large panicles ($\geq$ 100 mm) were 25, 2, 3, and 0%, respectively, for the same species (Figure 4).

Panicles lengths of all species tended to decrease as the date at which panicles were collected increased. However, considerable variability surrounded this trend. Low r^2 values associated with linear equations reflect this variability between maturity date and panicle length: *S. faberi,* L = 390 − 1.25 × DOY (r^2 = 0.52, P = 0.04); *S. viridis,* L = 184 − 0.52 × DOY (r^2 = 0.25, P = 0.16); and *S. pumila,* L = 190 − 0.55 × DOY (r^2 = 0.53, P = 0.02), where L represents panicle length (mm) and DOY is day of year for maturity. The tendency for decreasing panicle lengths with time probably reflected relatively late maturation of secondary and tertiary panicles as noted for *E. crus-galli* (Norris 1992a).

Although late-maturing panicles were shorter and produced fewer seeds, evidence for an effect of panicle maturity (collection date) on seed viability was equivocal. For example, linear equations describing the relationships between panicle collection dates and seed viability (V) had low r^2 and high P values: *S. faberi,* V = −164 + 0.91 × DOY (r^2 = 0.31, P = 0.19); *S. viridis,* V = 39 + 0.10 × DOY (r^2 = 0.07, P = 0.48); and *S. pumila,* V = −81 + 0.61 × DOY (r^2 = 0.34, P = 0.07).

Total Plot Seed Production

Estimates of total plot seed production obtained from the three simplified methods (panicle length, panicle averaging, and panicle frequency) are listed in Table 3, where they are compared to values derived from total panicle harvests. All of the simplified methods tended to estimate seed production reasonably well when seed production was high (> 1,000 seeds m^{-2}), typically being associated with average (of three to four replicates) deviations of < 50%. As seed production decreased below a few hundred seeds m^{-2}, however, deviations often were > 50%. The high deviations can be attributed to production of so few panicles (< 10 m^{-2}) that equations employing panicle size and number became unreliable.

The mean absolute deviation was lowest for the panicle length method (31%), which is logical, as this method most closely approximated actual counting of seeds on each individual panicle within a defined area. The panicle averaging method had the highest mean absolute deviation (67%), probably because errors in estimating seed production arose as a result of the nonlinear relationship between panicle

TABLE 3. Comparison of four methods of estimating production of viable seeds of *Setaria,* including herbicide-treated *S. viridis* (herb), during 1993 and 1994. Values represent averages from 6 to 8 plots (combined *Z. mays* and *G. max* plots). Average deviations of values derived from the panicle length (lgth.), averaging (avg.), and frequency (freq.) methods compared to the panicle harvest (harv.) method; e.g., −21 = underestimation by 21% compared to panicle harvest method.

	Estimation method							
	Panicle harv.		Panicle lgth.		Panicle avg.		Panicle freq.	
Species	1993	1994	1993	1994	1993	1994	1993	1994
	Seed m^{-2}							
S. faberi	3,730	108	3,981	58	4,940	112	4,753	72
S. viridis	6,831	1,297	6,678	1,050	8,075	1,179	6,129	963
S. pumila	3,888	182	2,981	166	4,826	227	3,758	190
S. viridis herb	745	154	563	352	1,880	154	369	30
	Deviation (%)							
S. faberi	NA[a]	NA	+2	−42	−50	+24	+44	−22
S. viridis	NA	NA	−11	−21	+24	−14	+37	−34
S. pumila	NA	NA	−21	−13	−21	−78	−11	+46
S. viridis herb	NA	NA	−6	+129	−325	+0	−16	−80
Mean absolute deviation			31		67		36	

[a] Abbreviation: NA, not applicable.

TABLE 4. Comparison of *Setaria faberi* seed production estimated by the Weibull panicle frequency method with values reported in an independent study of the effects of herbicide treatments on *S. faberi* panicle and seed production. Observed seed production m^{-2} was calculated by multiplying observed seeds $plant^{-1}$ by observed plants m^{-2} (Defelice et al. 1989).

Treatment[a]	Observed panicles				Observed seeds				Estimated seeds			
	1986	1987	1986	1987	1986	1987	1986	1987	1986	1987	1986	1987
	Plant−1		m^{-2}		$Plant^{-1}$		m^{-2}		$Plant^{-1}$		m^{-2}	
Untreated	2.2	3.9	34.9	160	460	600	8,050	26,400	542	961	8,595	39,405
Hand weeded	0.2	0	0.1	0	70	0	7	0	49	0	25	0
Bent + Seth 0.8 ± 0.2	3.5	3.8	1.7	53	630	770	315	13,706	862	936	419	13,053
0.6 ± 0.2	2.0	0	0.3	0	1,660	0	166	0	493	0	74	0
0.6 ± 0.1	2.2	2.2	0.8	7	700	340	210	1,734	542	542	197	1,724
Acif + Seth 0.3 ± 0.1	2.2	2.2	0.9	7	860	320	516	768	542	542	222	1,724
0.14 ± 0.1	3.0	5.1	1.7	16	760	1,070	456	3,424	739	1,256	419	3,941
Clor + Seth 0.005 + 0.1	1.0	4.0	0.1	26	540	560	162	2,856	246	984	25	6,403
0.002 + 0.1	3.5	4.9	1.1	16	1,020	800	408	2,560	862	1,207	271	3,941

[a] Herbicide treatments (Acif, Bent, Clor, and Seth) were aciflourfen (5-[2-chloro-4-(triflouromethyl)phenoxy]-2-nitrobenzoic acid) at 0.3 and 0.14 kg ai ha^{-1}, bentazon (3-(1-methylethyl)-(1H)-2,1,3-benzothiadiazin-4(3H)-one-2,2-dioxide) at 0.8 and 0.2 kg ai ha^{-1}, sethoxydim at 0.2 and 0.1 kg ai ha^{-1}, and chlorimuron (2-[[[[(4-chloro-6-methyoxy-2-pyrimidinyl)amino]carbonyl]amino]sulfonyl] benzoic acid) at 0.005 and 0.002 kg ai ha^{-1}.

length and seed number and the nonnormal (skewed) distribution of panicle lengths. The mean absolute deviation of the panicle frequency method was relatively low (36%), probably because it accounted for the skewed distribution of panicle lengths.

In absolute terms of seed production, large errors associated with small seed densities may not be too critical. For example, seed production of herbicide-treated *S. viridis* in 1994 was calculated to be 154 and 30 seeds m^{-2} with the panicle harvest and panicle frequency methods, respectively. Although the deviation associated with this latter method was high, −81%, the absolute difference in seed production (124 seeds m^{-2}) may be inconsequential in practice.

Comparisons with Literature Data

The equations used in the panicle frequency method of estimating *Setaria* seed production were derived from data generated in the plots that were used to test the predictive ability of the method. Consequently, some "circularity of reasoning" detracts from the demonstrated predictive ability of the method. A better test of the ability of the method to estimate *Setaria* seed production would be to compare seed densities listed in independent studies to estimates derived from the panicle frequency method. We found two reports in the literature where values were given for both panicle and seed densities of *S. faberi* growing in crops. Analogous reports for *S. viridis* and *S. pumila* were not located.

Defelice et al. (1989) studied *S. faberi* panicle and seed production in Missouri for 2 yr in crops of herbicide-treated and untreated *G. max.* We used their panicle densities (Defelice et al. 1989, p. 370) and our *panicle fecundity* (Table 1) and *panicle frequency* (Table 2) equations for *S. faberi* to estimate seed production in their study. We then compared their reported values for seed production to our estimates (Table 4). Observed and predicted values for *S. faberi* seed production were in close agreement. For example, in plots not treated with herbicides during 1986, observed seed production was 460 seeds $plant^{-1}$ and 8,050 seeds m^{-2}, and our estimates, based on the reported 2.2 panicles $plant^{-1}$ and 34.9 panicles m^{-2}, were 542 seeds $plant^{-1}$ and 8,595 seeds m^{-2}. Furthermore, because predicted seed production of herbicide-treated *Setaria* approached observed values, we concluded that the reported herbicide treatments did not affect panicle fecundity or panicle size frequency greatly. The reduced herbicide rates used in this Missouri study apparently affected *S. faberi* seed production primarily by reducing panicle numbers. Application of herbicides at label rates eliminated *Setaria* panicles. The panicle averaging method did not estimate seed production in Missouri (data not shown) as effectively as the panicle frequency method, especially at high panicle densities.

In another study of *S. faberi* seed production in *G. max,* Biniak and Aldrich (1986) reported panicle and seed numbers per plant for 10 herbicide treatments in Arkansas. We used their panicle numbers to estimate seed production per plant. Untreated plants had 15.4 panicles, which produced 3,167 seeds (Biniak and Aldrich 1986). Our estimate of seed production for untreated plants was 3,793 seeds. Observed and predicted seed production of herbicide-treated plants were similar (Table 5). As in the previous study (Defilice et al. 1989), herbicide treatments apparently had a much great-

TABLE 5. Comparison of *Setaria faberi* seed production estimated by the panicle frequency method to values reported in an independent study of the effects of herbicide treatments on *S. faberi* panicle and seed production (Biniak and Aldrich 1986).

Treatment[a]	Observed panicles	Observed seeds	Estimated seeds
	Number $plant^{-1}$		
Untreated	15.4	3,167	3,793
Glyphosate early	1.3	114	320
mid	6.2	1,322	1,527
late	6.3	2,205	1,552
Chlorflurenol early	19.3	2,040	4,753
mid	11.2	2,221	2,758
late	20.4	3,823	5,024
Chlorsulfuron early	7.3	935	1,798
mid	18.6	3,515	4,581
late	14.9	2,763	3,670

[a] Treatments were chlorflurenol (no WSSA name), chlorsulfuron (2-chloro-*N*-[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]benzenesulfonamide), and glyphosate (*N*-phospho-methyl)glycine), applied at early, mid, or late dates after anthesis with a roller applicator.

er effect on panicle numbers than on panicle fecundity. The panicle averaging method did not estimate seed numbers per plant in Arkansas (data not shown) as effectively as the panicle frequency method, especially at high panicle numbers per plant.

In a greenhouse study (Wall 1993), a Canadian accession of *S. viridis* produced 4.6, 6.9, and 7.4 panicles plant^{-1} and 707, 1,140, and 1,402 seeds plant^{-1} at maximum/minimum temperature regimes of 16/10, 22/16, and 28/22 C, respectively. For these same panicle numbers, the panicle averaging method resulted in seed numbers nearly twice as large as those observed. The panicle frequency method resulted in values of 1,113, 1,670, and 1,791 seeds plant^{-1}, which were similar to the observed values.

Our results demonstrate consistencies in the relationships between panicle size and seed number regardless of crop, year, weed density, and herbicide application for three *Setaria* species. The size structures of *Setaria* panicles were consistent across crops and years but were affected appreciably by applications of full label rates of postemergence herbicides. Panicle size also tended to decrease as the season of seed maturation progressed from mid-August to late September. In contrast, the proportion of apparently viable seeds on panicles was relatively stable during this same period. Finally, seed production of *S. faberi*, *S. viridis*, and *S. pumila* can be approximated through either of three simplified methods. The first method requires only measurements of panicle length of each panicle within representative unit-areas of a plot or field. This can be done before, during, or after seed dispersal. The second technique involves multiplication of average seed numbers per panicle by the number of panicles. The third method requires only simple counts of panicle densities within representative unit-areas of a plot or field. Where there is a need to estimate *Setaria* seed production, any of the methods can be useful, but the latter technique (panicle frequency method) appears to best replace previously considerable efforts devoted to field harvesting and laboratory separation and counting of *Setaria* panicles and seeds with simple and relatively accurate mathematical functions.

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